

Catalogue of American Amphibians and Reptiles.

Doan, T.M., A.M. Nowacki, and P.A. Roberts. 2012.
Dendrobates leucomelas.

***Dendrobates leucomelas* Steindachner**
Yellow Banded Poison Dart Frog,
Bumblebee Poison Dart Frog, Sapito Miner

Dendrobates leucomelas Steindachner 1864:260.
Type-locality, "Columbien" [= Colombia]. Holotype, Naturhistorisches Museum Wien (NHMW) 19188, an adult, collected by J. Natterer in 1851 (not examined by authors). See **Nomenclatural History**.

• **CONTENT.** No subspecies are recognized.

• **DEFINITION.** *Dendrobates leucomelas* is a relatively large *Dendrobates* with a SVL ranging from 30.5–37.5 mm. The skin of the back is smooth while the posterior belly and ventral surface of the thighs are rugose (Silverstone 1975). The fingers are free and end in large discs that are truncate with converging margins. The first finger is shorter than the second and the disk is smaller than the others. The toes are also free but with smaller disks than on the fingers (Rivero 1961). *Dendrobates leucomelas* is 1 of 2 species of dendrobatids that lack an omosternum (Silverstone 1975). The dorsal coloration is largely black dominated by 3 broad yellow transverse bands, but can be greenish-yellow or orange in some populations (Lötters et al. 2007). The yellow bands typically contain black spots, bands, or intrusions (Silverstone 1975). In some areas the bands are orange or yellow, becoming greenish yellow at the extremities. The ratio of black ground color and colored dorsolateral bands varies (Fuentes and Rodriguez-Acosta 1997). Ventral surfaces are black with occasional lateral intrusion of yellow from the dorsal surface or a yellow spot (Rivero 1961). The limbs are yellow spotted with black (Silverstone 1975). The advertisement call of a male is a relatively loud, monotonous, but musical trill (Lötters et al. 2003). The trill can last from a few seconds to several minutes and serves as an



FIGURE 1. Adult *Dendrobates leucomelas* from near Puerto Ayacucho, Venezuela (photograph by Carl J. Franklin).

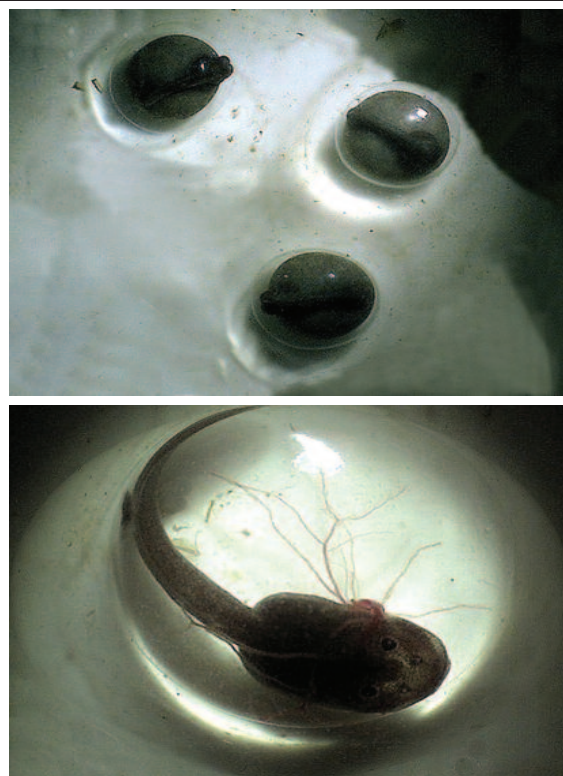


FIGURE 2. Eggs of *Dendrobates leucomelas* on day 5 (above) and day 15 (below) after oviposition in captivity (photographs by Perry A. Roberts).

advertisement call and as a courtship call (Summers 1992). The call consists of numerous (13–14 per second) pulsed, close-set notes that are similar in temporal structure and show slight upward frequency modification (Lötters et al. 2003).

• **DIAGNOSIS.** *Dendrobates leucomelas* and *Oophaga histrionica* are the only known dendrobatids that lack an omosternum, but this trait appears to represent convergent evolution, rather than a synapomorphy (Lötters et al. 2007). *Dendrobates leucomelas* can be distinguished by the presence of the wide, lightly colored transverse dorsal bands with intrusions and spots of the ground color. *Oophaga histrionica* typically lacks transverse dorsal bands and when they are present they do not have intrusions of the ground color (Silverstone 1975).

• **DESCRIPTIONS.** Forsman and Hagman (2006), Fuentes and Rodriguez-Acosta (1997), Lötters et al. (2007), Rivero (1961), and Silverstone (1975) provided descriptions of the coloration of *Dendrobates leucomelas*. Silverstone (1975) also described the skin texture and a little osteology. There are no published detailed descriptions of juveniles of this species. Lötters et al. (2003) described the advertisement call of a male and included an oscillogram and an audiospectrogram. Zimmerman and Zimmerman (1988) also presented an audiospectrogram.

• **ILLUSTRATIONS.** A picture of two adults and dia-

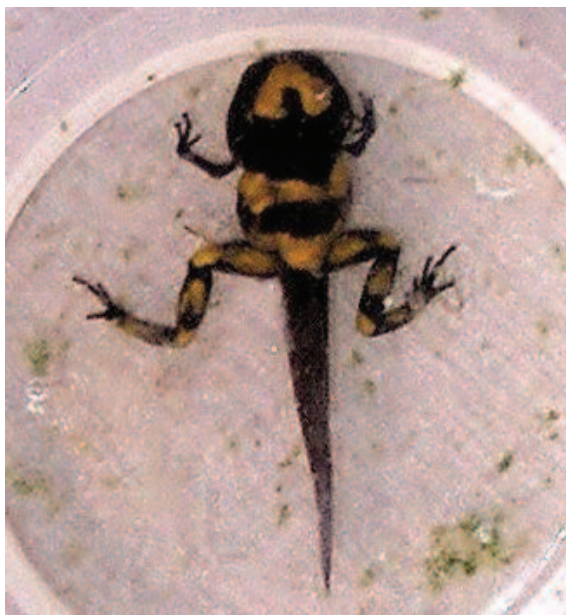
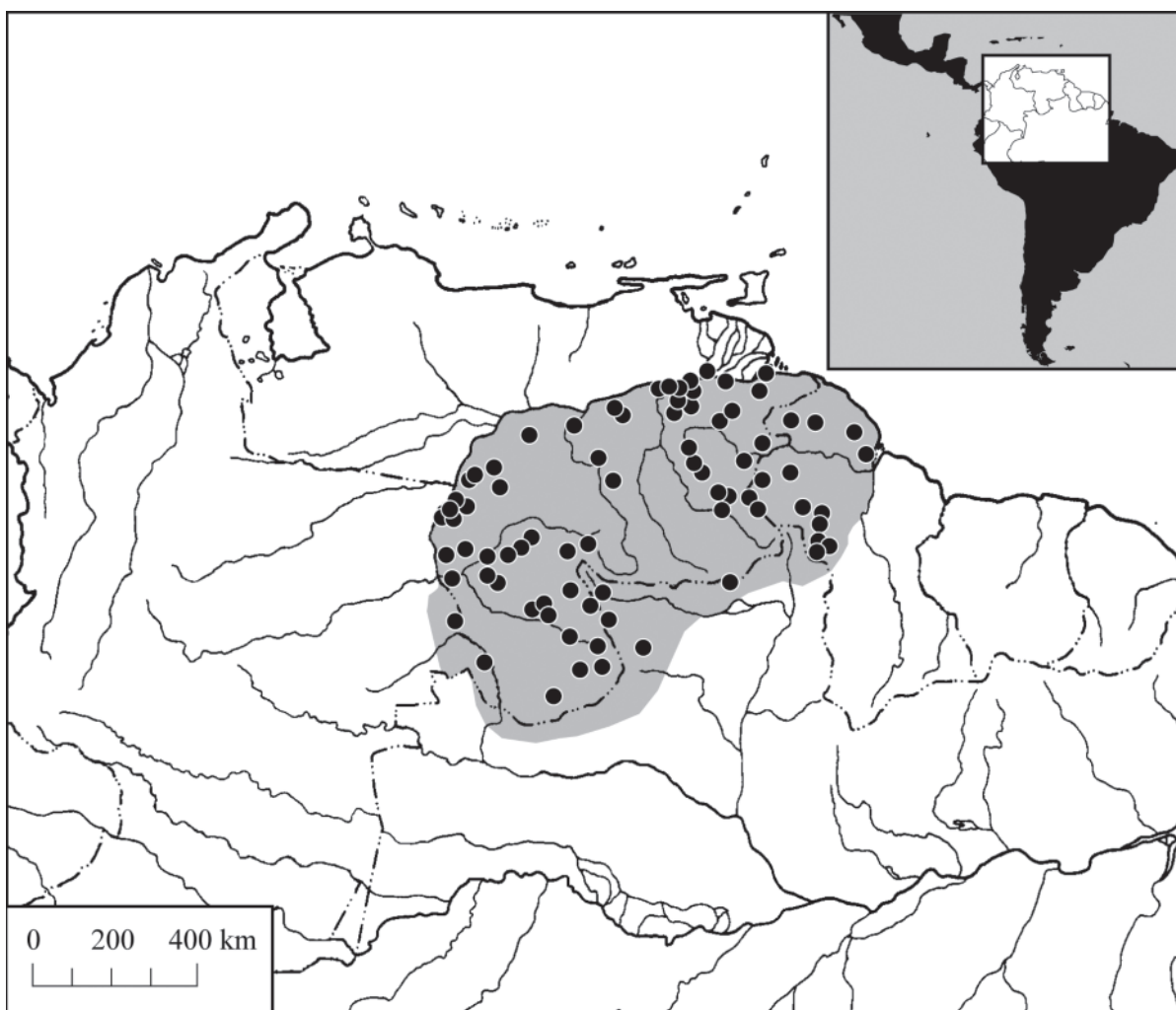


FIGURE 3. Metamorph of *Dendrobates leucomelas* on day 71 after oviposition in captivity (photograph by Perry A. Roberts).

grams of different spot patterns are provided by Fuentes and Rodríguez-Acosta (1997). Lötters et al. (2007) provided a series of color photographs depicting the varying color patterns of the species. Additional color photographs are in Bartlett (2003), Canela and Vásquez (1998), Gorzula and Señaris (1998), Gremone et al. (n.d.), Hoffmann-Röder and Krause (2004), Obst et al. (1988), Santos (2009), and Walls (1994). A color illustration appeared in Cogger and Zweifel (1998). A black-and-white photograph is provided by Duellman and Trueb (1986). Hoffmann-Röder and Krause (2004) provided structural diagrams of skin alkaloids. To date, there have been no published pictures of eggs or tadpoles.

• **DISTRIBUTION.** This species' range lies primarily in Venezuela. It is known from the western portion of the Guayana Shield and south, from the Guianan Orinoco drainage of Venezuela, north to the Río Orinoco, in the Bolívar and Amazonas States. The range expands south into northern Brazil (Roraima State), east to the Essequibo River in Guyana (Mazaruni Potaro District) and west into eastern Colombia (Guainía and Vichada Departments)



MAP. Distribution of *Dendrobates leucomelas*. The type-locality in eastern Colombia is unknown; dots mark known locality records. The indicated range is approximated.

(Lötters et al. 2007). Barrio and Fuentes (1998) provided a detailed map of the distribution of *D. leucomelas* in Venezuela; other maps can be found in Haffer (1979) and Hoogmoed (1979). It has been collected at elevations of 50–800 m (Silverstone 1975). The species inhabits lowland tropical moist forest and lowland tropical wet forest life zones (Silverstone 1975). It also persists in gallery forest within savannas (Hoogmoed and Gorzula 1979).

• **FOSSIL RECORD.** No fossils are known.

• **PERTINENT LITERATURE.** Relevant references are listed by topic: **behavior** (Pröhl 2005), **biochemistry** (Daly et al. 1978; de Magistris et al. 1985; Hoffmann-Röder and Krause 2004; Jackson 2009), **captive husbandry** (Forzán et al. 2008; Nogge 2004; Slavens and Slavens 1998; Weldon et al. 1993; Zimmermann 1989; Zimmermann and Zimmermann 1980, 1992, 1994), **conservation** (Goka et al. 2009; Gorzula and Señaris 1998; La Marca and Azevedo-Ramos 2004; Lawler et al. 2010; Lucy Hou et al. 2006; Molina et al. 2009; Nijman and Shepherd 2010; Rawson et al. 2011; van Andel et al. 2003; Zimmermann and Zimmermann 1992, 1994), **diet** (Silverstone 1975), **disease** (Koichigo et al. 2009), **distribution** (Barrio and Fuentes 1998; Duellman 1997, 1999; Fuentes and Rodríguez-Acosta 1997; Gorzula and Señaris 1998; Haffer 1979; Hoogmoed 1979; Lutz and Kloss 1952; Rivero-Blanco and Dixon 1979; Ruiz-Carranza et al. 1996; Silverstone 1975; Twomey and Brown 2008), **ecology and natural history** (Barrio-Amorós et al. 2010; Gorzula and Señaris 1998; Han 2008; Heyer and Barrio-Amorós 2009; Hoogmoed and Gorzula 1979; Lötters et al. 2007; Rivero 1961), **morphology** (Glaw and Vences 1997; Rada de Martínez and Bello de López 1996; Rivero 1961; Silverstone 1975), **parasitology** (Schrenzel et al. 2010), **phenotypic variation** (Fuentes and Rodríguez-Acosta 1997), **reproduction** (Brown et al. 2010; Forsman and Hagman 2006; Summers 1992), **speciation** (Noonan and Wray 2006), **systematics and phylogeny** (Clough and Summers 2000; Darst et al. 2005; Grant et al. 2006; Hagman and Forsman 2003; Jungfer and Böhme 2004; Lötters et al. 2003; Noonan and Gaucher 2006; Perez-Peña et al. 2010; Roberts et al. 2006; Santos 2009; Santos et al. 2003; Summers 1989; Summers and Clough 2001; Summers et al. 2001, 2002; Toft 1995; Vences et al. 2000; Wollenberg et al. 2006; Zimmermann and Zimmermann 1988), **toxins** (Aponte 2009; Daly et al. 1987, 2003; Saporito et al. 2004), **vocalization** (Erdtmann and Amézquita 2009; Lötters et al. 2003; Zimmermann and Zimmermann 1988), and **zoogeography** (Reinthal and Fistar 2002; Rivero 1964, 1967, 1971).

• **NOMENCLATURE HISTORY.** Considerable confusion exists regarding the authority to whom this taxon should be credited. Steindachner (1864) attributed the name *Dendrobates leucomelas* to Fitzinger without providing a published reference and listed *D. leucomelas* as a synonym of *D. tinctorius*. Silverstone

(1975) claimed that the species should be attributed to Fitzinger. Hoogmoed and Gorzula (1979) explained that because Fitzinger never published a description and did not work with Steindachner, and because Steindachner (1864) did provide a description, the author of the species should be Steindachner (1864). Hoogmoed and Gorzula (1979)'s clarification was followed by Barrio Amorós (1998), Roberts et al. (2006), and Lötters et al. (2007), but was not followed by Häupl et al. (1994).

• **ETYMOLOGY.** The species name, *leucomelas*, is Latin for “with white and black,” presumably a reference to the color pattern consisting of light and dark bands.

• **ACKNOWLEDGMENTS.** We thank Carl J. Franklin for his photograph of an adult *Dendrobates leucomelas*.

LITERATURE CITED

- Aponte, J.C. 2009. Multipronged Search for Pharmacologically Active Compounds: Amazonian Plants, Chalcones, Tetrahydrobenzothienopyrimidines and Beta-allenyl Esters. Unpubl. Ph.D. Diss., Univ. Louisville, Louisville, Kentucky.
- Barrio, C.L. and O. Fuentes. 1998. Distribución de *Dendrobates leucomelas* (Amphibia: Anura: Dendrobatidae) en Venezuela. *Acta Biol. Venezuelica* 18:35–41.
- Barrio-Amorós, C.L. 1998. Sistemática y biogeografía de los anfibios (Amphibia) de Venezuela. *Acta Biol. Venezuelica* 18:1–93.
- , J.C. Santos, and O. Jovanovic. 2010. A new dendrobatid frog (Anura: Dendrobatidae: *Anomaloglossus*) from the Orinoquian rainforest, southern Venezuela. *Zootaxa* (2413):37–50.
- Bartlett, R.D. 2003. Poison Dart Frogs. Facts & Advice on Care and Breeding. Barron's Educ. Ser.
- Brown, J.L., V. Morales, and K. Summers. 2010. A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *Am. Nat.* 175:436–446.
- Canela, J. and J. Vásquez. 1998. *Dendrobates*. *Reptilia* (GB) (2):18–25.
- Clough, M. and K. Summers. 2000. Phylogenetic systematics and biogeography of the poison frogs: evidence from mitochondrial DNA sequences. *Biol. J. Linn. Soc.* 70:515–540.
- Cogger, H.G. and R.G. Zweifel (eds.). 1998. *Encyclopedia of Reptiles and Amphibians*. 2nd ed. Academic Press, San Diego.
- Daly, J.W., G.B. Brown, M. Mensah-Dwumah, and C.W. Myers. 1978. Classification of skin alkaloids from Neotropical poison-dart frogs (Dendrobatidae). *Toxicon* 16:163–188.
- , H.M. Garraffo, T.F. Spande, V.C. Clark, J. Ma, H. Ziffer, and J.F. Cover, Jr. 2003. Evidence for an enantioselective pumiliotoxin 7-hydroxylase in dendrobatid poison frogs of the genus *Dendrobates*. *Proc. Natl. Acad. Sci. USA* 100:11092–11097.

- , C.W. Myers, and N. Whittaker. 1987. Further classification of skin alkaloids from Neotropical poison frogs (Dendrobatidae), with a general survey of toxic/noxious substances in the Amphibia. *Toxicol.* 25:1023–1095.
- Darst, C.R., P.A. Menéndez-Guerrero, L.A. Coloma, and D.C. Cannatella. 2005. Evolution of dietary specialization and chemical defense in poison frogs (Dendrobatidae): a comparative analysis. *Am. Nat.* 165:56–69.
- de Magistris, L., B. Annibale, G. Delle Fave, M. Salera, M. Puoti, E. Giordano, A. Forte, and V. Erspamer. 1985. Peptides of the APUD system in amphibian skins. *Peptides* 6 (Suppl. 3):203–208.
- Duellman, W.E. 1997. Amphibians of La Escalera Region, southeastern Venezuela: taxonomy, ecology, and biogeography. *Sci. Pap. Nat. Hist. Mus. Univ. Kansas* (2):1–52.
- . 1999. Distribution patterns of amphibians in South America, p. 255–328. *In* W.E. Duellman (ed.), *Patterns of Distribution of Amphibians: A Global Perspective*. Johns Hopkins Univ. Press, Baltimore.
- and L. Trueb. 1986. *Amphibian Biology*. McGraw-Hill, New York.
- Erdtmann, L. and A. Amézquita. 2009. Differential evolution of advertisement call traits in Dart-poison frogs (Anura: Dendrobatidae). *Ethology* 115: 801–811.
- Forsman, A. and M. Hagman. 2006. Calling is an honest indicator of paternal genetic quality in poison frogs. *Evolution* 60:2148–2157.
- Forzán, M.J., H. Gunn, and P. Scott. 2008. Chytridiomycosis in an aquarium collection of frogs: diagnosis, treatment, and control. *J. Zoo Wildl. Med.* 39:406–411.
- Fuentes, O. and A. Rodríguez-Acosta. 1997. The venomous “sapito minero” (*Dendrobates leucomelas* Steindachner, 1864) (Dendrobatidae), its medical importance and the phenotypic variations in specimens from two regions of the Amazonas state, Venezuela. *Acta Biol. Venezuelica* 17:53–57.
- Glaw, F. and M. Vences. 1997. Anuran eye colouration: definitions, variation, taxonomic implications and possible functions. *Herpetol. Bonn.* 1997: 125–138.
- Goka, K., J. Yokoyama, Y. Une, T. Kuroki, K. Suzuki, M. Nakahara, A. Kobayashi, S. Inaba, T. Mizutani, and A.D. Hyatt. 2009. Amphibian chytridiomycosis in Japan: distribution, haplotypes and possible route of entry into Japan. *Mol. Ecol.* 18:4757–4774.
- Gorzula, S. and J.C. Señaris. 1998. Contribution to the herpetofauna of the Venezuelan Guayana I. A data base. *Scientia Guayanæ* (8):xviii + 269 p., 129 pl., 2 maps.
- Grant, T., D.R. Frost, J.P. Caldwell, R. Gagliardo, C.F.B. Haddad, P.J.R. Kok, D.B. Means, B.P. Noonan, W.E. Schargel, and W.C. Wheeler. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bull. Amer. Mus. Nat. Hist.* (299): 1–262.
- Gremone, C., F. Cervigón, S. Gorzula, G. Medina, and D. Novoa. n.d. Fauna de Venezuela. Vertebrados. Ed. Biosfera, Caracas, Venezuela.
- Haffer, J. 1979. Quaternary biogeography of tropical lowland South America, p. 107–140. *In* W.E. Duellman (ed.), *The South American Herpetofauna: its Origin, Evolution, and Dispersal*. Mus. Nat. Hist. Univ. Kansas Monogr. (7).
- Hagman, M. and A. Forsman. 2003. Correlated evolution of conspicuous coloration and body size in poison frogs (Dendrobatidae). *Evolution* 57: 2904–2910.
- Han, X. 2008. Does Life History Shape Sexual Size Dimorphism in Anurans: A Comparative Analysis. Unpubl. Ph.D. Diss., Univ. Guelph, Guelph, Ontario, Canada.
- Häupl, M., F. Tiedemann, and H. Grillitsch. 1994. Katalog der Typen der Herpetologischen Sammlung nach dem Stand vom 1. Jänner. *Kat. Wiss. Samml. Naturhist. Mus. Wien* 9:1–42.
- Heyer, W.R. and C.L. Barrio-Amorós. 2009. The advertisement calls of two sympatric frogs, *Leptodactylus lithonaetes* (Amphibia: Anura: Leptodactylidae) and *Pristimantis vilarsi* (Amphibia: Anura: Strabomantidae). *Proc. Biol. Soc. Washington* 122:282–291.
- Hoffmann-Röder, A. and N. Krause. 2004. Synthesis and properties of allenic natural products and pharmaceuticals. *Angew. Chem. Intl. Ed.* 43: 1196–1216.
- Hoogmoed, M.S. 1979. The herpetofauna of the Guianan Region, p. 241–279. *In* W.E. Duellman (ed.), *The South American Herpetofauna: its Origin, Evolution, and Dispersal*. Mus. Nat. Hist. Univ. Kansas Monogr. (7).
- and S.J. Gorzula. 1979. Checklist of the savanna inhabiting frogs of the El Manteco region with notes on their ecology and the description of a new species of treefrog (Hylidae, Anura). *Zool. Meded.* 54:183–216.
- Jackson, L.D. 2009. Chiral Guanidine Catalyzed Enantioselective Protonation Reactions. Ph.D. Diss., Natl. Univ. Singapore.
- Jungfer, K.-H. and W. Böhme. 2004. A new poison-dart frog (*Dendrobates*) from northern central Guyana (Amphibia: Anura: Dendrobatidae). *Salamandra* 40:1–6.
- La Marca, E. and C. Azevedo-Ramos. 2004. *Dendrobates leucomelas*. *In* IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>.
- Lawler, J.J., S.L. Shafer, B.A. Bancroft, and A.R. Blaustein. 2010. Projected climate impacts for the amphibians of the Western Hemisphere. *Conserv. Biol.* 24:38–50.
- Lötters, S., K.-H. Jungfer, F.W. Henkel, and W. Schmidt. 2007. *Poison Frogs: Biology, Species & Captive Care*. Edition Chimaira, Frankfurt am Main.
- , S. Reichle, and K.H. Jungfer. 2003. Advertisement calls of Neotropical poison frogs (Amphibia: Dendrobatidae) of the genera *Colostethus*, *Dendro-*

- bates* and *Epipedobates*, with notes on dendrobatid call classification. *J. Nat. Hist.* 37: 1899–1911.
- Lucy Hou, P.-C., T.W. Shiau, M.-C. Tu, C.-C. Chen, T.-Y. Chen, Y.-F. T-sai, C.-F. Lin, and S.-H. Wu. 2006. Exotic amphibians in the pet shops of Taiwan. *Taiwania* 51:87–92.
- Lutz, B. and G.R. Kloss. 1952. Short notes on some frogs from the Upper Amazons and a few vicariant forms. *Mem. Inst. Oswaldo Cruz* 50:629–678.
- Molina, C., J.C. Señaris, M. Lampo, y A. Rial (eds.). 2009. *Anfibios de Venezuela: Estado del Conocimiento y Recomendaciones para su Conservación*. Inst. Zool. Ecol. Trop. (UCV), Fund. La Salle Cienc. Nat. (FLSCN), y Inst. Venez. Invest. Cien. (IVIC).
- Nijman, V. and C.R. Shepherd. 2010. The role of Asia in the global trade in CITES II-listed poison arrow frogs: hopping from Kazakhstan to Lebanon to Thailand and beyond. *Biodivers. Conserv.* 19: 1963–1970.
- Nogge, G. 2004. Jahresbericht 2003 der Aktiengesellschaft Zoologischer Garten Köln. *Z. Kölner Zoo* 47:1–32.
- Noonan, B.P. and P. Gaucher. 2006. Refugial isolation and secondary contact in the Dyeing Poison Frog *Dendrobates tinctorius*. *Mol. Ecol.* 15:4425–4435.
- and K.P. Wray. 2006. Neotropical diversification: the effects of a complex history on diversity within the poison frog genus *Dendrobates*. *J. Biogeogr.* 33: 1007–1020.
- Obst, F.J., K. Richter, and U. Jacob. 1988. *The Completely Illustrated Atlas of Reptiles and Amphibians for the Terrarium*. T.F.H Publ., Inc., Neptune City, New Jersey.
- Perez-Peña, P.E., G. Chavez, E. Twomey, and J.L. Brown. 2010. Two new species of *Ranitomeya* (Anura: Dendrobatidae) from eastern Amazonian Peru. *Zootaxa* (2439):1–23.
- Pröhl, H. 2005. Territorial behavior in dendrobatid frogs. *J. Herpetol.* 39:354–365.
- Rada de Martínez, D. and R. Bello de López. 1996. Estudio de la piel y escudetes dermicos de *Dendrobates leucomelas* (Amphibia, Dendrobatidae), p. 59–73. In J.E. Péfaur (ed.), *Herpetología Neotropical. Actas del II Congreso Latinoamericano de Herpetología*. II Vol. Consejo Publ., Univ. de Los Andes, Merida, Venezuela.
- Rawson, D.M., G. McGregor Reid, and R.E. Lloyd. 2011. Conservation rationale, research applications and techniques in the cryopreservation of lower vertebrate biodiversity from marine and freshwater environments. *Intl. Zoo Yrbk* 45:1–16.
- Reinthal, H.-P. and M.I. Fistar. 2002. Biodiversität und Zoogeographie der Amphibien Fauna von Caparo, Venezuela. *Linzer biol. Beitr.* 34:1267–1284.
- Rivero, J.A. 1961. Salientia of Venezuela. *Bull. Mus. Comp. Zool.* 12:1–207.
- . 1964. The distribution of Venezuelan frogs V, the Venezuelan Guayana. *Carib. J. Sci.* 4:411–420.
- . 1967. Anfibios coleccionados por la expedición Franco-Venezolana al alto Orinoco 1951–1952. *Carib. J. Sci.* 7:145–154.
- . 1971. Notas sobre los anfibios de Venezuela I. Sobre los hilidos de la Guayana Venezolana. *Carib. J. Sci.* 11:181–193.
- Rivero-Blanco, C. and J.R. Dixon. 1979. Origin and distribution of the herpetofauna of the dry lowland regions of northern South America, p. 281–298. In W.E. Duellman (ed.), *The South American Herpetofauna: its Origin, Evolution, and Dispersal*. Mus. Nat. Hist. Univ. Kansas Monogr. (7).
- Roberts, J.L., J.L. Brown, R. von May, W. Arizabal, A. Presar, R. Symula, R. Schulte, and K. Summers. 2006. Phylogenetic relationships among poison frogs of the genus *Dendrobates* (Dendrobatidae): a molecular perspective and increased taxon sampling. *Herpetol. J.* 16:377–385.
- Ruiz Carranza, P.M., M.C. Ardila-Robayo, and J.D. Lynch. 1996. Lista actualizada de la fauna de Amphibia de Colombia. *Rev. Acad. Colombiana Cienc. Exactas, Fis. Nat.* 20:365–415.
- Santos, J.C. 2009. *Phylogeography and the Evolution of Correlated Traits under Multiple Origins of Aposematism in the Poison Frog Family*. Ph.D. Diss., The University of Texas at Austin.
- , L.A. Coloma, and D.C. Cannatella. 2003. Multiple, recurring origins of aposematism and diet specialization in poison frogs. *Proc. Natl. Acad. Sci.* 100: 12792–12797.
- Saporito, R.A., H.M. Garraffo, M.A. Donnelly, A.L. Edwards, J.T. Longino, and J.W. Daly. 2004. Formicine ants: an arthropod source for the pumiliotoxin alkaloids of dendrobatid poison frogs. *Proc. Natl. Acad. Sci. USA* 101:8045–8050.
- Schrenzel, M.D., C.L. Witte, J. Bahl, T.A. Tucker, N. Fabian, H. Greger, C. Hollis, G. Hsia, E. Siltamaki, and B.A. Rideout. 2010. Genetic characterization and epidemiology of helicobacters in non-domestic animals. *Helicobacter* 15:126–142.
- Silverstone, P.A. 1975. A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. *Bull. Nat. Hist. Mus. Los Angeles Co.* (21):1–55.
- Slavens, F.L. and K. Slavens. 1998. *Reptiles and Amphibians in Captivity. Breeding – Longevity and Inventory current January 1, 1997*. Slaveware, Seattle, Washington.
- Steindachner, F. 1864. *Batrachologische Mittheilungen*. Verhandl. K. K. Zool.-Bot. Gesell. Wien 14: 239–288 + pls. 9–17.
- Summers, K. 1989. Sexual selection and intra-female competition in the Green Poison-dart Frog, *Dendrobates auratus*. *Anim. Behav.* 37:797–805.
- . 1992. Mating strategies in two species of dart-poison frogs: a comparative study. *Anim. Behav.* 43: 907–919.
- and M.E. Clough. 2001. The evolution of coloration and toxicity in the poison frog family (Dendrobatidae). *Proc. Natl. Acad. Sci. USA* 98:6227–6232.
- and D.J.D. Earn. 2008. The cost of polygyny and the evolution of female care in poison frogs. *Biol. J. Linn. Soc.* 66:515–538.
- , L.A. Weigt, P. Boag, and E. Bermingham. 1999. The evolution of female parental care in poison

- frogs of the genus *Dendrobates*: evidence from mitochondrial DNA sequences. *Herpetologica* 55: 254–270.
- Symula, R., R. Schulte, and K. Summers. 2001. Molecular phylogenetic evidence for a mimetic radiation in Peruvian poison frogs supports a Müllerian mimicry hypothesis. *Proc. R. Soc. Lond.* 268: 2415–2421.
- , —, and —. 2002. Molecular systematics and phylogeography of Amazonian poison frogs of the genus *Dendrobates*. *Mol. Phylo. Evol.* 26:452–475.
- Toft, C.A. 1995. Evolution of diet specialization in Poison-dart Frogs (Dendrobatidae). *Herpetologica* 51:202–216.
- Twomey, E. and J.L. Brown. 2008. Spotted poison frogs: rediscovery of a lost species and a new genus (Anura: Dendrobatidae) from northwestern Peru. *Herpetologica* 64:121–137.
- van Andel, T.R., A.V. MacKinven, and O.S. Bánki. 2003. Commercial Non-timber Forest Products of the Guiana Shield. An Inventory of Commercial NTFP Extraction and Possibilities for Sustainable Harvesting. The Future of Commercial NTFPs in Guyana. Netherlands Comm. IUCN, Amsterdam.
- Vences, M., J. Kosuch, S. Lötters, A. Widmer, K. Jungfer, J. Köhler, and M. Veith. 2000. Phylogeny and classification of poison frogs (Amphibia: Dendrobatidae), based on mitochondrial 16S and 12S ribosomal RNA gene sequences. *Mol. Phylo. Evol.* 15:34–40.
- Walls, J.G. 1994. *Jewels of the Rainforest – Poison Frogs of the Family Dendrobatidae*. T.F.H. Publ., Inc., Neptune City, New Jersey.
- Weldon, P.J., B.J. Demeter, and R. Roscoe. 1993. A survey of shed skin-eating (dermatophagy) in amphibians and reptiles. *J. Herpetol.* 27:219–228.
- Wollenberg, K.C., M. Veith, B.P. Noonan, and S. Lötters. 2006. Polymorphism versus species richness—systematics of large *Dendrobates* from the eastern Guiana Shield (Amphibia: Dendrobatidae). *Copeia* 2006:623–629.
- Zimmermann, E. and H. Zimmermann. 1992. Dart-poison frogs (Dendrobatidae): biology; breeding and conservation, p. 5–20. *In* M.J. Uricheck (ed.), 15th International Herpetological Symposium on Captive Propagation & Husbandry. Intl. Herpetol. Symp., Inc.
- and —. 1994. Reproductive strategies, breeding, and conservation of tropical frogs: dart-poison frogs and Malagasy poison frogs, p. 255–266. *In* J.B. Murphy, K. Adler, and J.T. Collins (eds.), *Captive Management and Conservation of Amphibians and Reptiles*. SSAR Contrib. Herpetol. (11).
- Zimmermann, H. 1989. Conservation studies on the 'dart-poison' frogs Dendrobatidae in the field and in captivity. *Intl. Zoo Yrbk.* 28:31–44.
- and E. Zimmermann. 1980. Durch Nachzucht erhalten: Der Baumsteiger *Dendrobates leucomelas*. *Aquar. Mag.* 14:211–217.
- and —. 1988. Ethotaxonomie und zoogeographische artengruppenbildung bei pfielgiftfröschen. *Salamandra* 24:125–160.

Tiffany M. Doan, Anthony M. Nowacki, Central Connecticut State University, Department of Biology, 1615 Stanley Street, New Britain, CT 06050, USA (tiffperu@yahoo.com) and (tony-nowacki@yahoo.com), and **Perry A. Roberts**, Tropical Jewels, 4739 University Way NE #1224, Seattle, WA 98105, USA (info@tropicaljewels.com).

Primary editor for this account, Andrew H. Price.

Published 30 April 2012 and Copyright © 2012 by the Society for the Study of Amphibians and Reptiles.
